CHAPTER 24

The role of palaeoecology in conserving African ecosystems

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ABSTRACT: Africa holds critical and unique biodiversity, but conservation is challenging because of the complexity of landscapes and their history, and the multitude of drivers and stakeholder perspectives. Palaeoecology can help in developing a nuanced understanding of landscape history that can inform pressing conservation issues, including climate change integrated conservation strategies, fire management, management of herbivores and rewilding, ecosystem restoration, sustainable use of natural resources, and management of cultural landscapes. To be useful, however, the data from palaeoecological proxies needs to be converted into metrics that are useful and accessible to conservationists and managers, requiring rigorous calibration against modern and instrumental data sets, alongside sound chronologies. Palaeoecologists can help in enhancing the applied value of their work by interpreting it in ways that are underpinned by sound ecological theory in ways that are relevant to pressing conservation questions. The design of projects and the interpretation and application of data can be used as starting points for interdisciplinary, collaborative approaches with stakeholders. Finally, the modelling of palaeoecological data can help stakeholders to explore landscape changes and the effect of management interventions under different scenarios of climate and land-use change in the future.

24.1 INTRODUCTION

Africa's landscapes are home to important biodiversity hotspots as well as the world's only intact megafaunal assemblage (Archer *et al.* 2018). They are also characterised by a large rural population, whose livelihoods directly depend on ecosystem services, alongside rapidly changing socio-economic contexts that include urbanisation and development. Conservation in Africa takes place both inside and outside of protected areas and both approaches present challenges and opportunities. Developing conservation strategies that benefit both biodiversity and people depends on developing and understanding of landscape history both in terms of ecological variability and cultural context.

In the early days of conservation, the idea of maintaining, preserving or restoring 'balance' was prevalent, and ideas of equilibrium were also reflected in early ecological theory. Maintaining populations at fixed carrying capacity was an approach common in southern Africa, while in East Africa strict preservation of 'wilderness' – areas perceived, often wrongly, to have been little modified by people – was a dominant conservation ideal (Gillson 2015). Added to this, many colonial governments perceived fire to be destructive and implemented policies of fire suppression, disrupting traditional burning practices, such as seasonal mosaic burning (Gillson *et al.* 2019). However, more recent approaches to conservation accept that variability, flux and disturbance are normal to most populations and landscapes, and this raises a need for a long-term

perspective that allows managers to explore resilience and variability over centennial-millennial timescales.

Many African National Parks were founded in the early decades of the twentieth century, when ecosystems were likely to have been in an atypical state. Though most African landscapes have been managed by people for millennia, the combined impacts of fire suppression, removal or disruption of traditional management, and the decimation of megafaunal populations from the 19th century are likely to have led to atypically higher tree density in savannas. This high tree density is likely to be further exacerbated by the effects of CO₂ fertilisation, which benefits C₃ plants such as savanna trees and shrubs, more than C₄ plants, including savanna grasses, and is likely to play a role in bush encroachment (Bond and Midgley 2012; Midgley and Bond 2015; Wigley *et al.* 2009). On the other hand, some savannas were cleared of trees because of charcoal production or to make way for agropastoralism, and woody vegetation subsequently recovered following land abandonment (Blair *et al.* 2018; O'Connor *et al.* 2014). Therefore, interplay between environmental change and the role of anthropogenic influence, both positive and negative, are important aspects of landscape history that needs to be considered in conservation planning and ecosystem management.

Amid all of this complexity, science is only part of the basis for conservation decisions, while stakeholder values, cultural context and local perspectives must also be considered (Rogers *et al.* 2013). A central challenge that palaeoecologists can contribute to is developing nuanced, interdisciplinary and inclusive understanding of landscape history (Marchant and Lane 2014; Marchant *et al.* 2018; Mustaphi *et al.* 2019), that can then be applied in defining and refining conservation and management goals (Gillson 2015; Githumbi *et al.* 2020; Wolfe *et al.* 2007). Here I discuss the role of palaeoecology in understanding and managing the drivers of landscape changes, then identify some ways forward in applying this knowledge to conservation practice.

24.2 UNDERSTANDING, PREDICTING AND MANAGING THE DRIVERS OF LANDSCAPE CHANGE

24.2.1 Climate

Past warm periods such as the African Humid Period and the Mediaeval Warm Period can provide valuable insights into the response of ecosystems to climate change, as well as the feedbacks between fire, climate and vegetation structure (Lüning *et al.* 2017). They have a particularly important role in informing and refining the development of models that simulate changes in vegetation cover based on climatic and other variables. This has been demonstrated in work modelling the greening of the Sahara during the mid-Holocene. Palaeoecological data indicated that models based on orbital forcing alone were under-estimating the magnitude and extent of the greening event (Lézine *et al.* 2011; Pausata *et al.* 2020; Tierney *et al.* 2017). This helped in shaping more complex models that include for example feedbacks between vegetation and climate (Chen *et al.* 2020; Pausata *et al.* 2020; Rachmayani *et al.* 2015).

Most predictions of future climate change agree that Africa's climate will get warmer, but there is a high degree of uncertainty regarding future changes in rainfall. While it is commonly expected that warmer climates bring higher rainfall due to increased ocean evaporation, this is not always the case, and some areas are expected to experience aridification and/or increased extreme events (Engelbrecht *et al.* 2013; Pinto *et al.* 2018). This is of critical importance to areas where agriculture is rain fed and already marginal (Pohl *et al.* 2017). Reconstructing past climates and particularly the interaction between temperature and rainfall can help in understanding the interactions between regional climate systems and assist in more accurate downscaling of global models (Lüning *et al.* 2018). Furthermore, palaeoecological data can help in understanding vegetation-climate-fire feedbacks that in turn shape the distribution of fire-adapted ecosystems

(Bond and Midgley 2012). It can also inform the manipulation of drivers such as fire that interact with climate. Information such as this is critical in designing conservation strategies that consider climate change, for example, potential shifts in the distribution of ecosystems and species as well as identifying populations that are likely to be most vulnerable or most resilient to climate change (Hannah *et al.* 2002). In a world of finite space and limited conservation resources, a sound basis for conservation prioritisation in a changing climate is critical (Foden *et al.* 2019).

24.2.2 Fire

Fire is a critical component of many African ecosystems, and is essential in maintaining grasslands, savannas and heathlands in areas of sub-Saharan Africa that have rainfall that is high enough to support forest (Bond *et al.* 2005). Nevertheless, fire management remains a contested issue in many areas, due to risk to property and life, as well as due to lack of understanding of its important ecological role (Bowman *et al.* 2013; Gillson *et al.* 2019). Many colonial governments believed fire to be detrimental and implemented policies of fire suppression in ecosystems that were naturally fire adapted (Moura *et al.* 2019). Later, when attempts to suppress fire proved futile, these policies were replaced by prescribed burns at regular intervals (van Wilgen *et al.* 2014). Policies of fire suppression and prescribed burning disrupted traditional fire management and homogenised the fuel load, leading to artificially intense and widespread fires in subsequent decades (Humphrey *et al.* 2020).

People have managed fire for millennia, for example by patch mosaic burning, which involves burning small patches of vegetation starting in the early dry season (Laris 2011). As different patches are burned at different times, this creates patches of vegetation with different post-fire ages (time since burned). Species assemblages often change throughout post-fire succession, and therefore a heterogeneous mosaic of different post-fire ages provides a wider range of habitat, biodiversity and ecosystem services than would be present had only a single, large fire occurred (Parr and Brockett 1999). In addition, such skilful management of fire helps to prevent late season wildfires that homogenise the landscapes (Humphrey *et al.* 2020), and can be used to manipulate the balance of forest and savanna elements at the savanna-forest ecotone (Fairhead and Leach 1996).

Palaeoecology is essential in understanding the impacts of anthropogenic fire management and the effects of fire suppression and management. Such records can in addition contribute to debates of anthropogenic 'savannisation' and the extent of human influence on forest ecosystems (Veldman 2016; Willis *et al.* 2004). Studying fire history through the charcoal record can help in determining whether current fire policies are within the historical range of variability. They may also assist in reinstating the skillful management of fire by communities who have incorporated fire management into their livelihoods for millennia (Humphrey *et al.* 2020).

24.2.3 Herbivory

Herbivores have both direct and indirect effects on vegetation structure and composition through physical impact on plant biomass and their influence on ecosystem processes, such as nutrient cycling and seed dispersal (Cromsigt *et al.* 2018). Changes in herbivore density thus have major implications for ecological function and biodiversity conservation (Hempson *et al.* 2015). Hunting, disease and manipulation of carnivore populations have all altered wild and domestic herbivore numbers, leading to declines in population size and distribution of many wild species in the late 19th and early 20th centuries (Venter *et al.* 2017). In southern Africa, reports of vast herds of wildebeest and springbok were reported in the early 20th century, while such herds have vanished from today's landscapes (Home 1874; Skead *et al.* 2007; Venter *et al.* 2017). In the 20th century, there have also been wide fluctuations in populations of both wild and domestic herbivores in response to, for example, changes in domestic and local markets for meat and wool,

intensification of agriculture, a transition to game farming, as well as illegal hunting of rhino and elephant (Beinart 2003). These changes would have directly affected vegetation structure and composition and influenced nutrient cycling, physical disturbance and fire regimes through changes in biomass accumulation.

The use of coprophilous fungal spores is commonly used to pinpoint the timing and effects of megafaunal extinctions (Burney *et al.* 2003; Feranec *et al.* 2011), but there are also possibilities for addressing ecological questions about changes in herbivore abundance and how they affected vegetation on more recent timescales of decades to centuries (Ekblom and Gillson 2010; Goethals and Verschuren 2019). This information is invaluable in informing the management and restoration of functional herbivore-driven landscapes (Fuhlendorf *et al.* 2009). It could also play a role, alongside pollen data, in addressing questions about the impacts of elephants on their habitat, specifically whether elephant impact on trees is unprecedented due to their confinement in small areas, or whether the loss of tree cover is actually a return to the less wooded landscapes of the 17th and 18th century (Gillson 2015; Veldman 2016).

With urbanisation continuing apace in Africa, and the effects of government grants on rural livelihoods, game farming and re-wilding are likely to become increasingly attractive options for conservation (Hoogendoorn *et al.* 2019) (though the effects of the current COVID-19 pandemic on these options remain to be seen (Lindsey *et al.* 2020)). Palaeoecologists can help managers decide what should the landscapes look like, and how many herbivores there should be (Hempson *et al.* 2015; Venter *et al.* 2017).

24.2.4 Anthropogenic Influence

Many African National Parks were founded in the early decades of the twentieth century, a time when many landscapes had been affected by intensive human impact including changes in fire and fauna as well as changing climate and rising CO₂, and as well as changes in land use including sedentarisation (i.e. loss of transhumant lifestyles) and land abandonment. There is therefore a role for palaeoecology, specifically fossil pollen and phytolith analysis, in exploring variability in ecosystem structure and composition, particularly in terms of woody vegetation density. These data allow ecosystem managers to distinguish, for example, whether increasing tree cover is a recovery from past tree clearance or an unprecedented loss of open, grassy savanna (Gillson 2015; Gillson and Marchant 2014; Parr *et al.* 2014). As mentioned above, palaeoecological data can also help in understanding the role of past management of fire and herbivores, and the effects of disruption of traditional fire management (Humphrey *et al.* 2020).

24.3 CHALLENGES IN APPLICATION OF PALAEOECOLOGY TO BIODIVERSITY CONSERVATION IN AFRICA

Despite the great potential for synergy between palaeoecology and conservation, practical collaboration between the two fields remains rare. Here I will identify some challenges for palaeoecology and suggest some ways forward for increasing the application of our work.

24.3.1 Calibration

Palaeoecological data as it is presented in Quaternary journals is not easy for conservation managers to use (Davies *et al.* 2014). They need to be translated into metrics that are more closely aligned with ecological parameters and ecosystem services that are usually the target of management goals (Davies and Bunting 2010; Gillson and Marchant 2014). For example, a measure of changes in tree density is much more useful in conservation than a measure of arboreal pollen abundance (Gillson and Duffin 2007). Therefore, good calibration is needed

between palaeo-proxies and ecological parameters, but calibration remains a major and barely addressed issue in palaeoecological studies of most African ecosystems (Julier *et al.* 2018). Accurate calibration that includes a measure of confidence limits will allow translation of pollen data to estimates of changing vegetation composition that are much more useful to managers. Much more work is needed in this regard, especially in Africa, where quantitative, multi-proxy data could be invaluable in understanding the feedbacks occur between climate, vegetation, fire and herbivory (Julier *et al.*, 2021, this volume).

The same can be said of charcoal and spore data. Charcoal can be invaluable for reconstructing fire history, but it is also notoriously difficult to interpret, requiring comprehensive calibration efforts (Adolf *et al.* 2018). This is partly because different fire intensities affect the completeness of combustion and different fuel sources (e.g. grass versus woody vegetation) and thus their representation in the charcoal record (Leys *et al.* 2017). Amalgamation and meta-analyses of multiple charcoal data sets via the Global Charcoal data base can help in quantifying the relationship between biomass burning and charcoal representation (Hawthorne *et al.* 2018; Marlon *et al.* 2016). Emerging techniques such as Fourier Transform Infrared Spectroscopy can help in unravelling the complexity between fire intensity and charcoal representivity (Gosling *et al.* 2019). Similarly, studies suggest that *Sporomiella* alone do not seem to accurately represent herbivore density in African ecosystems (Baker *et al.* 2013). A suite of spore proxies is needed, and more quantitative work is required to relate these to herbivore biomass and if possible to different herbivore guilds (Feranec *et al.* 2011; Goethals and Verschuren 2019).

As well as the use of modern data sets, there is also potential for calibrating palaeoecological data against instrumental records of climate change (Jacques *et al.* 2015; Vallè *et al.* 2018), satellite imagery of fire, e.g. the MODIS data set (Adolf *et al.* 2018) and historical records of herbivory numbers fire (Baker *et al.* 2013, van Asperen *et al.* 2020).

24.3.2 Chronologies and influx rates

Calibration against instrumental records requires detailed and accurate chronologies, in order to compare measured changes in historical and palaeoecological records. Where such chronologies are available, pollen influx rates can be used. Influx rates have advantages over both percentage data, which are influenced by the Fagerlind effect (Fagerlind 1952), and concentration data, which are influenced by changes in sediment accumulation rate. In the case of pollen percentages, the change in the abundance of any particular plant will affect the abundance of all other taxa present, because the total pollen sum always has to be 100%, regardless of how much biomass is present in the landscape. Similarly, a faster (slower) rate of sediment accumulation may lead to reductions (increases) in pollen concentration, even if the abundance of a plant in the landscape has not changed. However, such detailed chronologies are rarely found in palaeoecological data from semi-arid areas, where there are often hiatuses in sediment accumulation due to extended dry periods, and bioturbation by large mammals. In such cases, influx rates are not reliable, but careful comparison of percentage and concentration data can assist interpretation. There can be more confidence that trends observed in both percentage and concentration data reflect real changes in plant abundance (Baker *et al.* 2013; Forbes *et al.* 2018).

24.3.3 Taxonomic resolution

A further challenge in the application of fossil pollen data in biodiversity conservation is taxonomic resolution. Important ecological changes with implications for biodiversity conservation often occur at the species and genus level. For example, loss of species is a major concern for conservationists and changes in habitat quality, such as a shift from palatable to unpalatable grasses can have conservation management implications. Complementary proxies e.g. phytoliths can help to resolve poorly resolved but ecologically important families such as the Poaceae (Bremen

et al. 2019). Further, detailed work is needed on the pollen morphology and associated ecological affinity of taxa within diverse families, such as the Asteraceae, containing both generalist and specialist species (Blackmore *et al.* 2010). Environmental DNA from sediments (sedaDNA) is increasingly used to provide accurate taxonomic resolution (Bálint *et al.* 2018; Clarke *et al.* 2019), though further work is needed to improve coverage of African species in genomic databases (Dommain *et al.* 2020).

24.3.4 Engagement with ecological theory

Increasing the use of palaeoecology in conservation requires that palaeoecologists engage with relevant theoretical and management frameworks. The shift from ‘balance of nature’ to ‘flux of nature’ as the underlying paradigm in ecology, has had profound implications for conservation (Gillson 2015; Pickett *et al.* 1997). Specifically, managing ecosystems and populations that are not at equilibrium requires a different approach to old approaches to conservation that aimed to prevent change. Ecosystem management emerged in response to develop conservation approaches that accepted the heterogeneous, dynamic nature of ecosystems (Grumbine 1997). Working with variable ecosystems in which disturbance and change are normal, raises the need for information on variability over ecologically relevant timescales, in order to define conservation goals that are based on processes rather than states (Gillson 2015). Many ecosystems are dynamic and fluctuate in response to disturbance and environmental change, however long-term data are needed to help managers to identify when ecosystems are approaching ‘tipping points’ or novel states. There is a natural synergy between palaeoecology and resilience theory (Davies *et al.* 2018), in that hypotheses generated regarding resilience and thresholds in ecosystems can potentially be tested using palaeoecological data (Gillson *et al.* 2020; Seddon *et al.* 2011).

24.3.5 Theory to application: relevance to current conservation questions

Once palaeoecological data is calibrated into forms that are recognisable to ecologists and managers, there still remains the challenge of how to apply these data to current conservation questions. As well as climate-changed-integrated conservation strategies, mentioned above, an important interface between conservation practice and palaeoecological data is establishing acceptable limits of variation in key parameters such as woody vegetation cover, herbivore density and fire regimes. Recent trends in such parameters can be compared against data spanning decades and centuries, helping to quantifying the historical range of variability and the extent of intensifying human management, including the impact of changes in fire and fauna as well as land use implemented by colonial governments (Gell *et al.* 2012; Hoffman *et al.* 2019). Measures of the long-term variability can help to identify unprecedented change from normal background variability (Keane *et al.* 2009). Thus, long-term data from palaeoecology can help to understand the ecological character of an ecosystem. For example, palaeoecological data could potentially be incorporated into definitions of ecological characters, limits of acceptable change and Thresholds of Potential Concern (TPCs) (Gell 2010; Gillson and Duffin 2007).

Knowledge of long-term change is central to restoration ecology and rewilding. In restoration ecology, conservationists need to have a reference state (Falk 2017; Higgs *et al.* 2014; Nogué *et al.* 2017). While this is often a nearby undisturbed or little disturbed site, such locations are not always available. Indeed, even those that are perceived to be undisturbed may have a more complex history than can be gleaned from present day conditions (Forbes *et al.* 2018; Gell 2010). Thus, restoration targets including the rewilding of ecosystems requires data from before the intensive human impact of the 18th and 19th century. On the theme of restoration, there is a tendency to view grassy and other open ecosystems as less valuable than forests or woody systems, therefore their afforestation is prioritised (Bond *et al.* 2019; Parr *et al.* 2014). This tendency

has become even more pronounced given recent drives to encourage tree planting as a means of enhancing carbon storage (Bastin *et al.* 2019). In some cases, where forest cover has become denuded or degraded, reforestation with native species can enhance biodiversity conservation and carbon storage at the same time (Lewis *et al.* 2019). In others, however, ancient grasslands and heathlands have been mistakenly identified as degraded or anthropogenically derived (Bond *et al.* 2019; Parr *et al.* 2014). This has led to inappropriate afforestation schemes that threaten rare open landscapes that are home to unique biodiversity (Bond *et al.* 2019; Veldman 2016; Veldman *et al.* 2019). Palaeoecology should therefore support the protection of open ecosystems and in the design of appropriate forest restoration programmes while at the same time raising the profile of ancient grasslands and heathlands as valid conservation targets.

A further step in the translation of palaeoecological data for conservation purposes is to convert them to indices for ecosystem services, such as biodiversity, sediment regulation, soil stability, sediment quality, and water quality (Dearing *et al.* 2012). This approach can help engage stakeholders by alerting them to changes in key services, information which could potentially inform sustainable management of natural resources, but to date has rarely been applied in Africa.

24.3.6 Integrating with other disciplines and knowledge streams

A multiproxy approach that helps to elucidate the complexities of landscape history and people's role in shaping the environment can help to build a nuanced and inclusive understanding of landscape history that can provide cultural and local context for interpreting change and informing future sustainable management (Gillson 2015; Githumbi *et al.* 2020; Marchant and Lane 2014; Mustaphi *et al.* 2019; Richer and Gearey 2018). Though much palaeoecological research occurs in the lab and behind the microscope, a key component of our work can be in collaborating with stakeholders and listening to stakeholder perspective on ecosystem change (Wolfe *et al.* 2007). Projects can be co-designed with stakeholders with their management needs and goals in mind (Rogers *et al.* 2013; Wolfe *et al.* 2007). Palaeoecologists can attend conservation conferences and workshops where managers and ecologists articulate questions that can be usefully addressed using palaeoecological techniques, or arranging consultations with community groups (Davies *et al.* 2014; Wolfe *et al.* 2007). Where palaeo-projects are already underway, it is useful to meet with communities, government, parastatals and NGOs while in the field, explain the potential utility of the palaeoecological data and to explore questions of mutual interest.

After a project's completion, it is useful to provide results in more than one format. Scientific publications are not always the most accessible or useful way in communicating results to stakeholders, formats such as reports, poster, or stakeholder feedback workshop might be more convenient. Such workshops are especially valuable when stakeholders can help in shaping elements of the project e.g. in adding insights to possible feedbacks between drivers and/or in utilising project outputs such as model-based tools that allow them to explore the effects of different scenarios or fire, herbivory and climate (Capitani *et al.* 2019; Hossain *et al.* 2020). Stakeholders often have different perspectives on how ecosystem change affects their livelihoods and there are often important cultural components of landscape change that can only be captured through consultation with stakeholders.

24.3.7 The importance of modelling and future scenarios

Reconstructing the past does not always provide analogues for the future (Williams and Jackson 2007). We face unprecedented rates of climate change and human impact, as well as social and economic structures that differ vastly from the past, as well as potentially novel combinations of climate parameters and anthropogenic stressors that may produce ecological surprises (Lindsey

et al. 2020; Williams and Jackson 2007). Nevertheless, understanding past ecological dynamics can help to elucidate the interactions and processes that drive ecosystem change. Building models based on palaeoecological data that simulate past interactions between key drivers and responders e.g. vegetation, climate, fire and herbivory provides a basis for exploring future scenarios, especially where palaeoecological proxies have been turned into Ecosystem Service Indicators (see above) (Dearing *et al.* 2012; Perry *et al.* 2016).

Models based on palaeoecological data can simulate past interactions between human and environmental factors, for example, climate, fire, herbivory and vegetation (Perry *et al.* 2016). Such models can then be parameterised using current and future scenarios. Furthermore, some modelling approaches, such as system dynamics models offer opportunities for combining insights from long-term data with local knowledge of ecosystem change, complexity and likely future scenarios (Hossain *et al.* 2020). This has the twofold advantage of improving the relevance and applicability of palaeoecology whilst also improving access to a diverse range of voices in scenario planning and conservation management. Though highly uncertain, such models can help stakeholders to explore different possible future scenarios of land cover and ecosystem services (Caves *et al.* 2013).

24.4 CONCLUSIONS

Africa's landscapes are dynamic and complex, and managing them requires flexible and adaptive conservation approaches that safeguard biodiversity as well as providing ecosystem services and respecting indigenous knowledge. This means embracing a past-present-future perspective that includes a knowledge of ecosystem variability, ecological function as well as cultural heritage and the role of traditional management. There is thus enormous potential for better integration of palaeoecological and other long-term data into biodiversity conservation and natural resource management.

Carrying out palaeoecological research in Africa has some challenges, however, including the lack of sites and poor pollen preservation in semi-arid areas and the sheer diversity of the flora in forested areas. Despite this, the discipline has enormous potential value in conserving African biodiversity, especially as landscape history is often not well understood. Fine resolution studies covering the late Holocene are especially valuable to conservationists in understanding the impacts of climate change, the role of fire and herbivory, the effects of human management and the resilience of ecosystems. To realise this value, however, we in the palaeo-community must do our best to make our data accessible, and to present it in forms that are relevant to conservation. Aligning multiple proxies can help in distinguishing climatically driven from anthropogenically driven changes and provide the basis for defining restoration targets and thresholds of potential concern. Ensure that our research process is inclusive can contribute to building a nuanced and interdisciplinary understanding of landscape history that informs biodiversity conservation and the sustainable and equitable management of natural resources.

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